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# Atyid shrimps (Decapoda, Atyidae) from Tongguling National Nature Reserve, Hainan, China, with description of a new species

Jiping Zhang[1*], Junjie Hou[1*], Jinjin Fan[2], Yixinran Xu[1], Qinghua Chen[3], Zhaoliang Guo[1]

1 *School of Animal Science and Technology, Foshan University, Foshan 528231, Guangdong Province, China*
2 *Guangzhou Zhengbai Biotechnology Co., Ltd, Guangzhou 510700, Guangdong Province, China*
3 *South China Institute of Environmental Sciences, Ministry of Ecology and Environment, Guangzhou 510520, Guangdong Province, China*

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Corresponding authors: Qinghua Chen (chenqinghua@scies.org); Zhaoliang Guo (zlguo@fosu.edu.cn)

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## Abstract

Extensive field surveys of atyid shrimps in Tongguling National Nature Reserve, Hainan, China, led to the collection of three *Caridina* species: *C. lanceifrons* Yu, 1936, *C. elongapoda* Liang & Yan, 1977, and *C. tonggulinensis* **sp. nov.** Among them, *C. tonggulinensis* **sp. nov.** is described as a new landlocked species with a highly restricted distribution. Morphological and molecular analyses indicate a close affinity between the new species and *C. breviata* Ng & Cai, 2000. Nevertheless, the two species can be distinguished by several diagnostic characteristics, including the armature of the rostrum, the shape and proportions of the endopod of the male first pleopod, and egg size. Phylogenetic analyses based on partial mitochondrial 16S rRNA and COI gene sequences (453 bp and 489 bp, respectively) provide robust support for the distinct species status of *C. tonggulinensis* **sp. nov.** An overview of the general ecology, biology, economic significance, and conservation status of the three species is also included.

## Key Words

16S, COI, integrative taxonomy, morphology, new species, Tongguling National Nature Reserve

## Introduction

Hainan, an island surrounded by the South China Sea, was separated from the mainland by the Qiongzhou Strait approximately 65 million years ago (Liang 2018). Hainan Island is a biodiversity hotspot within the South-Central China region (Myers et al. 2000), whose exceptional biodiversity—characterized by abundant endemic species—stems from its dynamic geological evolution and climatic variability, combined with spatially heterogeneous habitats spanning marine, brackish, and freshwater ecosystems (Huang et al. 2023). *Caridina* H. Milne-Edwards, 1837, is the largest genus within the family Atyidae, comprising over 350 valid species distributed globally, except for Antarctica, with the majority found in the Indo-Pacific region (De Grave et al. 2023; Kunjulakshmi and Prakash 2025). Despite their small size, these shrimp, which are abundant in many freshwater habitats, provide important socio-economic benefits by serving as a local food source, poultry feed, and a valuable commodity in the aquarium trade (Holthuis 1980; Liang 2004; Guo et al. 2022; Hou et al. 2024). *Caridina* species play a significant role in freshwater ecosystems by serving as critical intermediaries in food webs, transferring energy from periphyton and detritus to higher trophic levels (Crowl et al. 2001; Weber and Traunspurger 2016).

The publication of two studies (Hou et al. 2024, 2025), which describe 10 new species, has raised the number of recorded *Caridina* species on Hainan Island to 19. This represents a significant update to the previous tally reported in prior works (Yu 1936, 1938; Liang and Yan 1983; Liang 2004; Cai 2014). Despite this progress, the taxonomic investigation of freshwater shrimp in Hain-

* These authors contributed equally to this work.

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an remains far from complete. Given the current understanding of their distribution patterns and the existence of substantial knowledge gaps, it is highly likely that many more *Caridina* species await discovery in this region.

In the face of a severe biodiversity crisis and the ongoing sixth mass extinction, the establishment of protected areas is an essential strategy and a fundamental defense (Watson et al. 2014; Hill et al. 2015). Tongguling National Nature Reserve (TNNR) was established in 2003. It is designated to protect the unique tropical evergreen monsoon dwarf forest ecosystem and its dependent rare wildlife, typical marine abrasion landforms, and offshore coral reef resources. The reserve is home to a remarkable diversity of life. Current records document 984 species of plants and 163 species of animals. Of these, 18 species—comprising mammals, birds, and amphibians—are listed under China's National Grade II Key Protected Animals (Quan et al. 2009; Tang and Xue 2022). Although freshwater shrimp were historically unrecorded in TNNR, three *Caridina* species (*C. lanceifrons* Yu, 1936, *C. elongapoda* Liang & Yan, 1977, and an unknown species) were discovered in a recent survey, constituting the first record of atyid shrimp diversity in the reserve. Integrated morphological, molecular, and phylogenetic evidence from our research demonstrates that the unknown species is new.

# Materials and methods

## Study area

Tongguling National Nature Reserve (19°36'54"N –19°41'21"N, 110°58'30"E–111°03'00"E) is located on the east coast of Wenchang City, Hainan Island, and is surrounded by the sea on three sides. It has a tropical monsoon climate, with an annual mean temperature of 23.9 °C and annual precipitation of 2361.3 mm. TNNR covers an area of 44 km$^2$, with a core area of 18.95 km$^2$ (Fig. 1B). There are 18 peaks in TNNR, with the main peak reaching 338.2 m above sea level, making it the highest peak in the northeast of Hainan Island (Zhan et al. 2015; Tang and Xue 2022). The soil type is mainly brick-red soil formed from granite and sandstone, with a shallow layer and a low degree of development. The vegetation types are mainly low-mountain dwarf rain forest, foothill shrub forest, coastal sandy vegetation, and mangrove. Several small streams and ditches are distributed throughout the reserve and represent the upper reaches of the Baoling River, which flows into the sea from the west. These streams tend to be short and steep. Many streams are ephemeral or have subsurface flow during the drier months.

## Specimen collection and deposition

During 2022 and 2024, we conducted fieldwork and sampling at eight sites in the Baoling River, streams, and ditches of TNNR (Fig. 1B, Table 1). Shrimp samples were obtained from microhabitats including banks, submerged leaf litter, aquatic vegetation, marginal vegetation, rocky substrates, and woody debris. The tools used to collect shrimps included a sturdy, long-handled, fine-meshed dip net (mesh size 0.6 mm). Sampling activities were documented using photo-

**Table 1.** Sampling locality data and species collected at each site in Tongguling National Nature Reserve, Hainan (ANC: ammonia nitrogen content; DO: dissolved oxygen; WP: water pH).

| Site | Coordinates | Date of sampling | ANC | DO | WP | Altitude | Microhabitat profile | Water current | Composition |
|---|---|---|---|---|---|---|---|---|---|
| | | | mg/L | mg/L | pH | m | | | Species |
| 1 | 19°40'10"N, 111°1'11"E | 8 Apr. 2023 | 0.02 | 6 | 7.6 | 230 | Rocky | Slow | *C. tonggulinensis* sp. nov., *Apotamonautes hainanensis*, *Neotiwaripotamon whiteheadi* |
| 2 | 19°40'14"N, 111°1'8"E | 20 Mar. 2023 | 0.01 | 6 | 7.5 | 167 | Rocky | Slow | *C. tonggulinensis* sp. nov., *Apotamonautes hainanensis*, *Neotiwaripotamon whiteheadi* |
| 3 | 19°40'12"N, 111°1'2"E | 20 Aug. 2023 | 0.04 | 5 | 7.5 | 154 | Rocky, mud, sand | Slow | *C. tonggulinensis* sp. nov., *Apotamonautes hainanensis*, *Neotiwaripotamon whiteheadi* |
| 4 | 19°40'15"N, 111°1'15"E | 25 Jan. 2024 | 0.06 | 5 | 6.8 | 37 | Rocky, mud, leaf litter | Intermediate | *C. tonggulinensis* sp. nov., *Apotamonautes hainanensis*, *Neotiwaripotamon whiteheadi*, *Hainanpotamon fuchengense* |
| 5 | 19°40'28"N, 111°1'3"E | 25 Jan. 2024 | 0.05 | 5 | 6.7 | 11 | Sand, mud, leaf litter | Slow | *C. tonggulinensis* sp. nov., *Apotamonautes hainanensis*, *Hainanpotamon fuchengense* |
| 6 | 19°39'27"N, 111°1'7"E | 25 Jan. 2024 | 0.02 | 6 | 7.2 | 43 | Sand, mud, leaf litter | Intermediate | *C. lanceifrons*, *Apotamonautes hainanensis* |
| 7 | 19°40'12"N, 111°0'40"E | 25 Jan. 2024 | 0.05 | 6 | 7.2 | 20 | Mud, leaf litter, aquatic plants | Intermediate | *C. lanceifrons*, *Macrobrachium nipponense*, *Gambusia affinis*, *Oreochromis niloticus* |
| 8 | 19°40'51"N, 111°0'57"E | 25 Jan. 2024 | / | / | / | 10 | Rocky, sand | Intermediate | *C. elongapoda*, *Palaemon debilis*, *Metapenaeus ensis* |

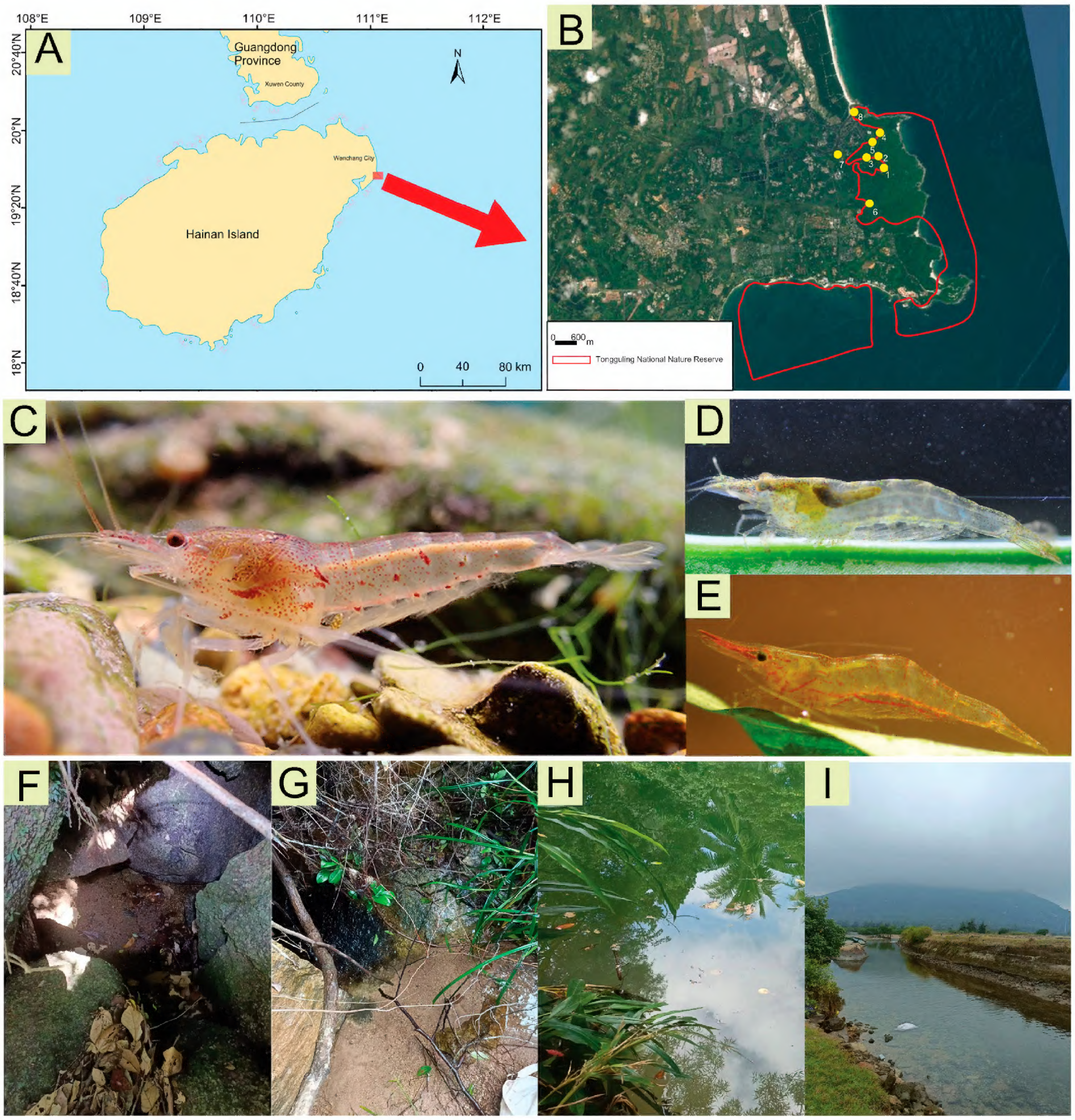


**Figure 1.** Distribution of collection sites, live coloration of shrimps, and their habitats. **A.** The map of Hainan Island; **B.** Collection sites in Tongguling National Nature Reserve, Hainan; **C.** Live coloration of *Caridina tonggulinensis* sp. nov.; **D.** Live coloration of *C. lanceifrons* Yu, 1936; **E.** Live coloration of *C. elongapoda* Liang & Yan, 1977; **F.** Habitat of *C. tonggulinensis* sp. nov. at site 1; **G.** Habitat of *C. tonggulinensis* sp. nov. at site 3; **H.** Habitat of *C. lanceifrons* at site 7; **I.** Habitat of *C. elongapoda* at site 8.

graphs and video recordings. Specimens were placed in oxygenated polythene bags, anesthetized with ice, and transported back to the hotel, after which they were photographed and fixed in 95% ethanol. Ethanol was replaced with fresh 75% ethanol after 24 h. The specimens were then transferred to 95% ethanol for further morphological examination and molecular analysis. All preserved material has been deposited in the South China Sea Institute of Oceanology, Chinese Academy of Sciences (CAS), China.

## Morphological study

Specimens were examined using a stereomicroscope (Olympus SZX7). Morphometric measurements of selected characters and illustrations were obtained using a digital camera (DP22) mounted on a stereomicroscope (Olympus SZX7) and Olympus CellSens Entry v1.18 software.

The following abbreviations are used throughout the text: TL, total length (measured from the rostral tip to the posterior margin of the telson); cl, carapace length

(measured from the postorbital margin to the posterior margin of the carapace); rl, rostral length (measured from the rostral tip to the postorbital margin); al, altitude; stn, sampling station. All measurements are in millimeters. Notation for the rostral formula follows Chace and Bruce (1993).

## Molecular analyses

Genomic DNA was extracted from abdominal muscle tissue using the Easy-Pure Genomic DNA Kit (TransGen Biotech, Beijing, China), following the manufacturer's instructions. Two loci were selected for analysis: cytochrome c oxidase subunit I (COI; Folmer et al. 1994) and the 16S ribosomal RNA gene (16S rRNA; von Rintelen et al. 2007). The primers used for COI amplification were LCO1490 (GGTCAACAAATCATAAAGATATTGG) and HCO2198 (TAAACTTCAGGGTGACCAAAAAATCA); for 16S rRNA, primers were 16S-F-Car (TGCCTGTTTATCAAAAACATGTC) and 16S-R-Car1 (GAAAGATAGAAACTAACCTGGCT). These primer pairs were used to amplify all *Caridina* specimens in this study, with two outgroup species (*Neocaridina palmata* Shen, 1948 and *Macrobrachium rosenbergii* De Man, 1879) included for comparison. PCRs were conducted in 50 µL reaction volumes.

PCR reactions were performed in 50 µL volumes using a Bio-Rad T100™ Thermal Cycler. The reaction mixture contained 25 µL of 2× EasyTaq Mix, 20 µL of $ddH_2O$, 2 µL each of the forward and reverse primers, and 1 µL of DNA template. The PCR amplification protocol consisted of 35 cycles of denaturation at 94 °C for 30 s, annealing at 46 °C for 60 s, and extension at 72 °C for 60 s, followed by a final extension at 72 °C for 5 min. Amplification products were verified by 1.5% agarose gel electrophoresis using 5 µL of each PCR product. Successfully amplified products were sequenced bidirectionally using an Applied Biosystems 3730 Analyzer (Applied Biosystems, Foster City, CA, USA), and consensus sequences were generated by verifying complementary strands.

For phylogenetic analyses, sequences of the new species and other *Caridina* species known from adjacent regions were included. All nucleotide sequences were aligned using the MUSCLE algorithm implemented in MEGA 7.0 (Kumar et al. 2016). Aligned COI and 16S sequences were trimmed to final lengths of 489 bp and 453 bp, respectively. The GTR + G + I model was selected as the optimal substitution model for both loci based on the Akaike Information Criterion (AIC) in jModelTest. The two loci were concatenated using the Concatenate Sequence function in PHYLOSUITE 1.2.3.

Phylogenetic trees were reconstructed from the concatenated dataset using maximum likelihood (ML) analysis in MEGA 7.0 (Kumar et al. 2016). ML analyses were conducted with two gene partitions (COI and 16S) under the GTR + G + I model, and branch support was assessed using 1,000 bootstrap replicates. Genetic distances were calculated using MEGA 11 (Stecher et al. 2020; Tamura et al. 2021). All new sequences generated in this study have been deposited in GenBank (see Table 2).

## Conservation status

The conservation status of the shrimp species treated herein was assessed in accordance with the *Guidelines for Using the IUCN Red List Categories and Criteria* (IUCN; https://www.iucnredlist.org/). These guidelines evaluate a species' extinction risk in the near term through assessments of its geographic distribution, population trends, and existing as well as projected threats.

## Taxonomy

**Family Atyidae De Haan, 1849**
**Genus *Caridina* H. Milne Edwards, 1837**

### *Caridina elongapoda* Liang & Yan, 1977

*Caridina nilotica elongapoda* Liang & Yan, 1977: 220, figs. 5–8 [Type locality: Xinzai, Gulei village, Zhangpu County, Fujian, southern China].
*Caridina nilotica elongapoda*.—Liang & Zheng, 1988: 15
*Caridina elongapoda*—Wowor et al., 2004: 341, fig. 6A, B.—Cai & Shokita, 2006: 249 (part?).—Cai et al., 2007: 285; Cai et al., 2009: 68.—Cai, 2014: 214; 2020: 1414, fig. 5.—de Mazancourt et al., 2018: fig. 2. —de Mazancourt et al., 2023: fig. 2.
*Caridina* aff. *brachydactyla*—Yeo, Cai & Ng, 1999: 218, figs 10–14.
Non *Caridina longirostris*—Chace, 1997: fig. 6 (part?).
*Caridina longirostris* — Liang, 2004: 195, fig. 94.

**Material examined.** CHINA – **Hainan Island** • 3 ♂♂, cl 2.9–3.3 mm, (CAS5713019); 4 ♀♀ (1 ovigerous), cl 3.1–5.0 mm, (CAS5713020), Baoling River, Tongguling National Nature Reserve, Longlou Town, Wenchang City, 19°40'51"N, 111°0'57"E, al. 10 m, stn. 8, coll. HOU J. J., 25 Jan. 2024.

**Remarks.** The taxonomic status of *Caridina elongapoda* has been discussed by Cai and Shokita (2006) and Cai (2014). Morphologically, our specimens match the original descriptions and illustrations by Liang and Yan (1977), as well as the redescription provided by Wowor et al. (2004) and Cai and Shokita (2006).

*C. elongapoda* is an amphidromous species that produces numerous small eggs (0.35–0.40 × 0.19–0.23 mm). These develop into extended planktotrophic larval stages capable of long-distance dispersal via oceanic currents, facilitating a broad distribution across Southeast Asia.

Owing to its striking appearance—a considerable size (up to 4 cm TL), a translucent body adorned with vibrant red patterns—and its slender, delicate shape, and planktonic swimming, *C. elongapoda* has attracted

**Table 2.** Specimens of atyid taxa used for DNA sequencing.

| Species | Specimen catalog | GenBank COI | GenBank 16S | Collection data | References |
|---|---|---|---|---|---|
| *Caridina ablepsia* | FU416700002 | PV535551 | PV541512 | Yongshun, Hunan, China | Hou et al. 2025 |
| *Caridina baoting* | HN1008 | PQ901512 | PQ932204 | Baoting, Hainan, China | Hou et al. 2025 |
| *Caridina breviata* | FU529236002 | PV535549 | PX269290 | Taishan, Guangdong, China | Hou et al. 2025 |
| *Caridina brevilineata* | FU5714026 | PV940554 | PV940425 | Qionghai, Hainan, China | Hou et al. 2025 |
| *Caridina caii* | FU5722002 | PV535542 | PV541503 | Wuzhishan, Hainan, China | Hou et al. 2025 |
| *Caridina cantonensis* | HN1011 | PQ901515 | PX248637 | Wenchang, Hainan, China | Hou et al. 2025 |
| *Caridina clinata* | FU5725002 | PV535540 | PV541501 | Ledong, Hainan, China | Hou et al. 2025 |
| *Caridina elongapoda* | CAS5713019 | PX471253 | PX471728 | Wenchang, Hainan, China | this study |
| *Caridina fontinalis* | FU5700002 | PV535547 | PV541508 | Haikou, Hainan, China | Hou et al. 2025 |
| *Caridina gracilipes* | CAS5713024 | PX457593 | PX588056 | Wenchang, Hainan, China | this study |
| *Caridina gracilirostris* | FU571521002 | PV535552 | PV541514 | Wanning, Hainan, China | Hou et al. 2025 |
| *Caridina haivanensis* | FU5500001 | PV940557 | PV940428 | Hai Van, Thua Thien-Hue, Vietnam | Hou et al. 2025 |
| *Caridina hepingensis* | FU5727009 | PV535546 | PV541505 | Qiongzhong, Hainan, China | Hou et al. 2025 |
| *Caridina huangi* | FU5727002 | PV535545 | PV541506 | Qiongzhong, Hainan, China | Hou et al. 2025 |
| *Caridina lanceifrons* | FU65 | MN701605 | MT446450 | Dongfang, Hainan, China | Xu et al. 2020 |
| | FU5727023 | PV940559 | PV940429 | Qiongzhong, Hainan, China | Hou et al. 2025 |
| | CAS5713021 | PX471252 | PX471727 | Wenchang, Hainn, China | this study |
| *Caridina lineatus* | HN1004 | PQ901508 | PQ932200 | Wanning, Hainan, China | Hou et al. 2024 |
| *Caridina macrophora* | FU538100002 | PV535553 | PV541515 | Nanning, Guangxi, China | Hou et al. 2025 |
| *Caridina minnanica* | FU5290001 | PV940560 | PV940430 | Jiangmen, Guangdong, China | Hou et al. 2025 |
| *Caridina qiongzhongensis* | FU5727017 | PV535544 | PV541507 | Qiongzhong, Hainan, China | Hou et al. 2025 |
| *Caridina serrata* | FU137 | MN701599 | MT446454 | Zhuhai, Guangdong, China | Chen et al. 2020 |
| *Caridina tetrazona* | FU, 2017-06-27-03 | MN701593 | PX149329 | Zhuhai, Guangdong, China | Chen et al. 2020 |
| *Caridina tonggulinensis* sp. nov. | CAS5713009 | PX626412 | PX600420 | Wenchang, Hainan, China | this study |
| | CAS5713010 | PX626413 | PX600421 | | |
| | CAS5713015 | PX6264134 | PX600422 | | |
| *Caridina tricincta* | FU532700001 | PV535550 | PV593959 | Longan, Guangxi, China | this study |
| *Caridina tunchengensis* | FU5716002 | PV535548 | PV541509 | Tunchang, Hainan, China | Hou et al. 2025 |
| *Caridina typus* | CAS Jap001 | PX471254 | PX471729 | Japan | this study |
| *Caridina wangan* | HN1001 | PQ901505 | PQ932198 | Wanning, Hainan, China | Hou et al. 2024 |
| *Caridina wenchangensis* | FU5713002 | PV535543 | PV541504 | Wenchang, Hainan, China | Hou et al. 2025 |
| *Caridina zhujiangensis* | HN1010 | PQ901514 | PQ932206 | Lingshui, Hainan, China | Hou et al. 2024 |
| *Macrobrachium rosenbergii* | RV_MI02 | MK113940 | MK113948 | Ruvu, Tanzania | Kuguru et al. 2019 |
| *Neocaridina palmata* | FUGX240821001 | PX248631 | PX248630 | Jingxi, Guangxi, China | Hou et al. 2025 |

significant attention in the ornamental trade. Although its coloration is less striking than that of *C. graciliros-tris* (the species commonly referred to as the "Red Nose Shrimp" internationally), this species is widely distributed along the coastal regions of China and easy to collect, thus appearing more frequently in the aquarium markets in China. Enthusiast breeders refer to it as the "Native Red Nose Shrimp".

**Coloration.** The transparent body is covered with fine red spots. Short, irregular, slanting red streaks appear on the ventral margin of the carapace, and a straight red line on the abdomen. The lower edge of the rostrum is crimson, and at times, the entire rostrum appears red. The peduncle of antennule is often reddish (Fig. 1E).

**Habitats.** In the vegetation of estuarines and the lower course of rivers.

**Distribution.** China, Vietnam, Malaysia, Indonesia, and the Philippines.

***Caridina lanceifrons* Yu, 1936**

*Caridina lanceifrons* Yu, 1936: 89, figs 5–7 [type locality: Haikou, Hainan Province, China];1938: 281, fig. 3.

*Caridina lanceifrons* — Dudgeon, 1985: 142; Liang & Yan, 1977: 15; Zheng, 1989: 6; Liang & Zhou, 1993: 231; Liang et al., 1993: 41; Li & Liang, 2002: 709; Cai, 2014: 217; Do et al., 2021: 15.

*Caridina flavilineata* Dang, 1975: 71, fig. 5 [type locality: Nam Ha, North Vietnam].

**Material examined.** 2 ♂♂, cl 2.7–2.8 mm, (CAS5713021), 3 ♀♀ (3 ovigerous), cl 4.4–4.9 mm, (CAS5713022), a pond in Tongguling National Nature Reserve, Longlou Town, Wenchang City, 19°40'12"N, 111°0'40"E, al. 20 m, stn. 7, coll. HOU J. J. and WU H., 25 Jan. 2024.

2 ♀♀, cl 4.1–4.4 mm, (CAS5713023), a stream in Tongguling National Nature Reserve, Longlou Town,

Wenchang City, 19°39'27"N, 111°1'7"E, al. 43 m, stn. 6, coll. HOU J. J. and WU H., 25 Jan. 2024.

**Remarks.** The morphological features of our specimens are consistent with previous descriptions (Yu 1936, 1938; Liang 2004; Cai 2014). Egg sizes vary slightly across the literature, with reported measurements of 0.74–0.84 mm × 0.56–0.61 mm (Yu 1938), 0.84–0.90 mm × 0.56–0.62 mm (Liang 2004), and 0.85–1.05 mm × 0.55–0.70 mm (Cai 2014), whereas they measured 0.81–0.88 mm × 0.48–0.53 mm in the present study. Therefore, *Caridina lanceifrons* exhibits intermediate reproductive traits, with medium-sized eggs and a moderate number of larval stages (Zheng and Liang 1992).

*C. lanceifrons* demonstrates notable resilience and broad environmental tolerance, allowing it to form abundant and dense populations across diverse brackish and freshwater habitats, including estuaries, rivers, streams, reservoirs, ponds, ditches, and rice fields. Its distribution extends from the southern coastal regions of China (Fujian, Guangdong, Hong Kong, Hainan, and Guangxi) northward to far inland central China (Hunan) (Liang 2004; Cai 2014) and also includes northern Vietnam and southern Thailand (Do et al. 2021).

In Wenchang, *C. lanceifrons* is of commercial importance and forms a key component of the diet of "saline-water ducks" traditionally reared in mangrove swamps. The ducks' diet is further supplemented by large-scale trapping of shrimp, which are used either for direct feeding or processed into a sun-dried additive. Dried shrimp is also widely sold in local markets, constituting a dietary staple for local residents.

**Coloration.** Body is translucent, colored from brownish to bluish, while females are typically a dark blackish-brown with a golden dorsal line running from the rostral tip to the last abdominal somite (Fig. 1D).

**Habitats.** In the vegetation of the estuaries, rivers, streams, reservoirs, ponds, ditches, and rice fields.

**Distribution.** China, Vietnam, and Thailand.

### *Caridina tonggulinensis* Hou, Zhang & Guo, sp. nov.

https://zoobank.org/66F8E1F7-1A30-4865-84F9-9F57C473B90E

Figs 1C, 2, 3

**Material examined.** CHINA - **Hainan Island** • ***Holotype*:** 1 ♂, cl 3.9 mm, (CAS5713007), a stream in Tongguling National Nature Reserve, Longlou Town, Wenchang City, 19°40'10"N, 111°1'11"E, al. 230 m, stn. 1, coll. HOU J. J., 8 Apr. 2023.

***Paratypes*:** 1 ♀, cl 4.7 mm, (CAS5713015), same collection data as holotype. 1 ♂, cl 3.6 mm, (CAS5713008); 1 ♂, cl 3.7 mm, (CAS5713009); 4 ♂♂, cl 2.5–3.1 mm, (CAS5713016), 7 ♀♀, cl 3.5–5.2 mm, (CAS5727014); 21 ♀♀, cl 2.5–4.4 mm, (CAS5727017), Tongguling National Nature Reserve, Wenchang City, 19°40'14"N, 111°1'8"E, al. 167 m, stn. 2, coll. HOU J. J., 20 Mar. 2023. 1 ♂, cl 3.8 mm, (CAS5713010), a stream in Tongguling National Nature Reserve, Longlou Town, Wenchang City, 19°40'12"N, 111°1'2"E, al. 154 m, stn. 3, coll. HOU J. J., 20 Aug. 2023. 6 ♂♂, cl 3.2–3.9 mm, (CAS5713012); 22 ♀♀, cl 3.9–5.5 mm, (CAS5727018), a stream in Tongguling National Nature Reserve, Longlou Town, Wenchang City, 19°40'15"N, 111°1'15"E, al. 37 m, stn. 4, coll. HOU J. J., 25 Jan. 2024. 1 ♂, cl 3.9 mm, (CAS5713011), 1 ♀ (ovigerous), cl 5.8 mm, (CAS5713013), a stream in Tongguling National Nature Reserve, Longlou Town, Wenchang City, 19°40'28"N, 111°1'3"E, al. 11 m, stn. 5, coll. HOU J. J., 25 Jan. 2024.

**Comparative material examined.** *Caridina breviata* Ng & Cai, 2000. CHINA - **Guangdong:** 1 ♂, cl 4.0 mm, (FU529236002); 2 ♂♂, cl 3.8–4.4 mm, (FU529236003), Haiyan Town, Taishan City, coll. HOU J. J., 25 May 2024; 1 ♂, cl 4.5 mm, (FU529425001), 1 ♀, cl 4.5 mm, (FU529425002), Enping City, Coll. HOU J. J. and FENG J. L., 20 Feb. 2025. *Caridina serrata* Stimpson, 1860. CHINA - **Guangdong:** 3 ♂♂, cl 3.2–3.8 mm, (FU5190001), Guishan Island, Zhuhai City, coll. GUO Z. L., 27 Nov. 2023. *Caridina baoting* Cai, 2014. CHINA - **Hainan Island:** 1 ♂, cl 4.9 mm, (FU5723001); 1 ♂, cl 5.3 mm, (FU5723002); 1 ♂, cl 4.3 mm, (FU5723003); 1 ♀, cl 4.8 mm, (FU5723004); 1 ♀, cl 5.1 mm, (FU5723005), stream from Xiangshui Town, Baoting County, 18°36'20"N 109°35'19"E, al. 361 m, coll. HOU J. J., 2 Jan. 2024.

**Description.** Body (Fig. 1C): Slender and sub-cylindrical, males up to 3.9 mm cl, females up to 5.8 mm cl. Sixth abdominal somite 0.36–0.49 (median 0.43, n = 8) times as long as carapace.

Rostrum (Fig. 2A, B): Rostrum short, straight, extension range: not beyond eye (29.85%, N = 67), beyond eye (44.78%, N = 67), to end of first antennular peduncle segment (14.92%, N = 67). Rostrum length (rl) 0.05–0.25 of cl (median 0.18, N = 67). Dorsally usually unarmed (95.52%, N = 67), rarely armed with 1–2 teeth (4.48%, N = 67); ventrally unarmed. Orbital margin posterior to carapace without teeth. Rostral formula: 0+0–2/0. lateral carina dividing rostrum into two unequal parts, continuing posteriorly to orbital margin.

Eyes (Fig. 2A): Well developed, on short ocular peduncle, cornea globular.

Carapace (Fig. 2A, B): Length 2.5–5.8 mm (median 4 mm, n = 67) in adult specimens. Smooth, glabrous; antennal spine acute, fused with inferior orbital angle; pterygostomian margin broadly rectangular, slightly produced forward; pterygostomian spine absent.

Antennule (Fig. 2C): Peduncle slightly shorter than scaphocerite; stylocerite reaching 0.74–0.80 (median 0.77, n = 3) times as long as basal segment; basal segment shorter than combined length of second and third segments, first segment 1.50–1.67 (median 1.59, n = 3) times as long as second segment, second segment 1.17–1.49 (median 1.32, n = 3) times as long as third segments; all segments with marginal plumose setae.

Antenna (Fig. 2D): Scaphocerite 2.7–3.2 (median 2.8, n = 3) times as long as wide.

First maxilliped (Fig. 2H): Palp of first maxilliped broadly triangular, ending in finger-like projection.

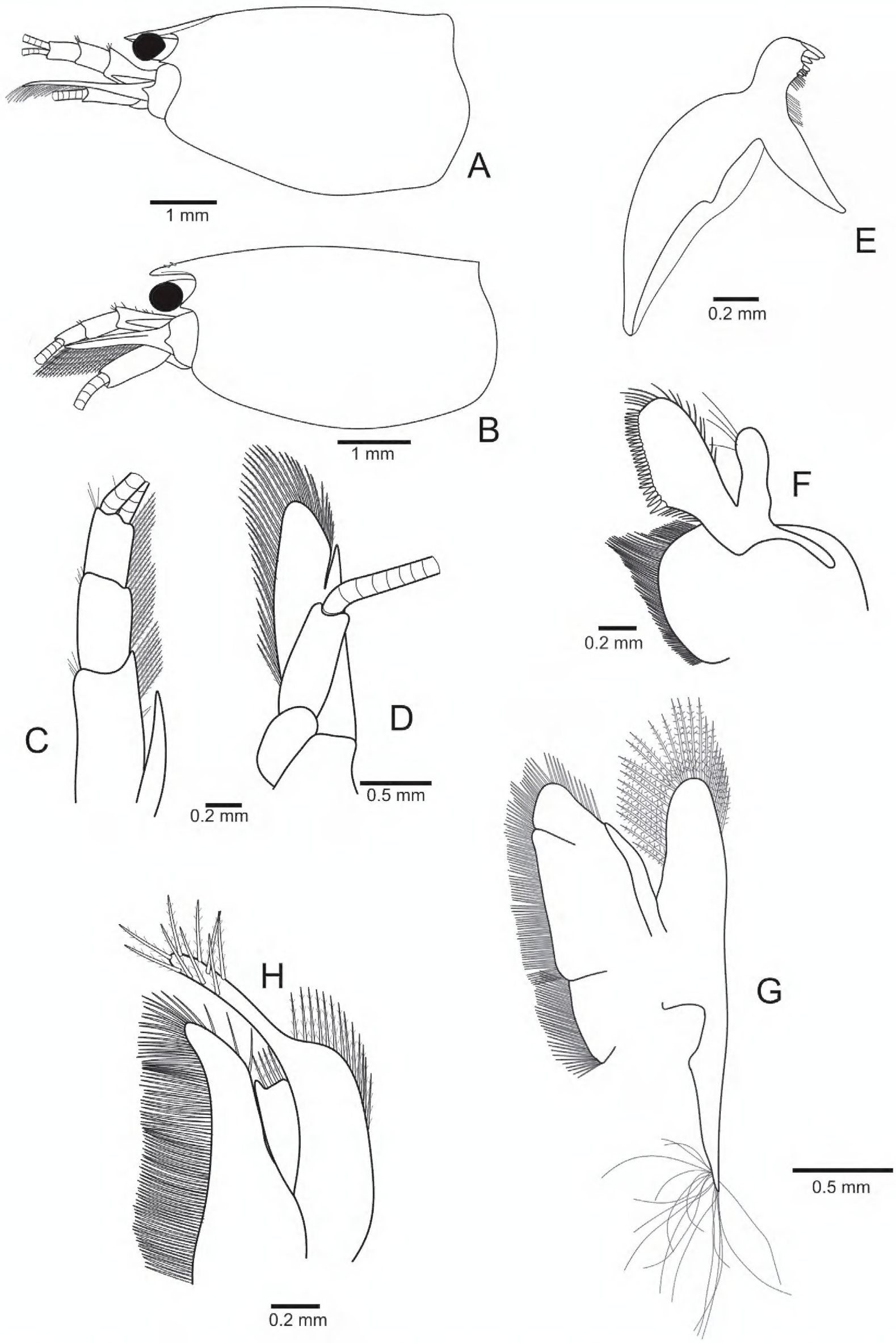


**Figure 2.** *Caridina tonggulinensis* Hou, Zhang & Guo, sp. nov.: **A.** Holotype male (CAS5713007); **B.** Paratype male (CAS5713011); **C–G.** Paratype male (CAS5713013). **A, B.** Cephalothorax; **C.** Antennular; **D.** Antenna; **E.** Mandible; **F.** Maxillula; **G.** Maxilla; **H.** First maxilliped.

Third maxilliped (Fig. 3B): Basal segment 1.10–1.22 (median 1.15, n = 3) times as long as penultimate segment; penultimate segment as long as distal segment.

First four pereiopods with epipod.

First pereiopod (Fig. 3C): Chela 2.00–2.29 (median 2.09, n = 5) times as long as high, 1.30–1.54 (median 1.33, n = 5) times as long as carpus; movable finger 2.16–3.74 (median 2.76, n = 5) times as long as wide and 0.71–1.26

(median 0.74, n = 5) times as long as palm, setal brushes well developed; carpus 1.22–1.92 (median 1.67, n = 5) times as long as wide, slightly excavated distally; merus 0.86–1.08 (median 1.03, n = 5) times as long as carpus.

Second pereiopod (Fig. 3D): Chela 2.62–2.88 (median 2.77, n = 5) times as long as high, 0.64–0.74 (median 0.66, n = 5) times as long as carpus; movable finger 3.92–4.97 (median 4.44, n = 5) times as long as wide, 1.23–1.80 (median 1.73, n = 5) times as long as palm, setal brushes well developed; carpus 5.69–6.53 (median 5.81, n = 5) times as long as wide, slightly excavated distally; merus 0.86–0.96 (median 0.94, n = 5) times as long as carpus.

Third pereiopod (Fig. 3E): Dactylus 2.81–4.01 (median 3.58, n = 5) times as long as wide, terminating in a prominent claw-like spine surrounded by simple setae, followed by 5–7 spiniform setae; propodus 3.24–4.29 (median 3.87, n = 5) times as long as dactylus, 8.78–10.30 (median 9.20, n = 5) times as long as wide; carpus 0.68–0.78 (median 0.75, n = 5) times as long as propodus; merus 1.74–1.94 (median 1.82, n = 5) times as long as carpus, with about 2–3 spiniform setae on the posterior margin.

Fourth pereiopod: Proportion and spination similar to third pereiopod.

Fifth pereiopod (Fig. 3F): Dactylus 3.86–5.26 (median 4.5, n = 5) times as long as wide, ending in prominent claw-like spine surrounded by simple setae, followed by a row of 33–42 spiniform setae; propodus 3.29–4.82 (median 3.99, n = 5) times as long as dactylus, 11.15–15.44 (median 12.62, n = 5) times as long as wide; carpus 0.56–0.67 (median 0.60, n = 5) times as long as propodus; merus 1.41–1.51 (median 1.42, n = 5) times as long as carpus, with about 2–3 spiniform setae on the posterior margin.

First pleopod (Fig. 3G): Endopod in male 0.53–0.60 (median 0.55, n = 4) times as long as exopod, sub-oval, 2.68–3.12 (median 2.78, n = 5) times as long as distally wide, tip rounded, inner margin either straight or lightly convex, long pappose setae on outer and distal margins, medium-length setae on inner margin; appendix interna well developed, arising from distal 0.33 of endopod, reaching slightly beyond end of endopod, distally with cincinuli.

Second pleopod (Fig. 3H): Appendix masculina rod-shaped, slightly thicker centrally, narrower distally, reaching about 0.57–0.68 (median 0.62, n = 5) times as long as exopod, bearing two rows of long spiniform setae, some short spiniform setae on basal part; appendix interna well developed, reaching 0.49–0.59 (median 0.52, n = 5) length of appendix masculina, distally with cincinuli.

Telson (Fig. 3I): Tapering posterior, with 4–5 pairs of short spiniform setae dorsal and one pair of short spiniform setae dorsolaterally; posterior margin 3–4 pairs of spiniform setae, lateral pair longer than intermediate pairs. Having a triangular protrusion at center of end.

Exopodite of the uropod (Fig. 3J) bears a series of 22–26 (n = 4) movable spinules along diaresis. The outermost spinule on the uropodial diaeresis is clearly overreaching the lateral spine.

Eggs: Ovigerous females with 26–35 eggs (mean 30, n = 5). Size of eye-developed eggs 0.60–0.66 mm × 1.00–1.10 mm (n = 6) in diameter.

**Remarks.** *Caridina tonggulinensis* sp. nov. resembles *C. breviata* Ng & Cai, 2000, in the short rostrum and the proportions among the joints of the second, third, and fifth pereiopods (cf. Ng and Cai 2000). However, it can be separated from *C. breviata* by the shape and proportions of the endopod of the male first pleopod (sub-oval, 2.68–3.12 times as long as wide vs. sub-triangular, 2.10 times as long as wide in *C. breviata*); the longer appendix masculina and appendix interna of the male second pleopod (appendix masculina 0.57–0.68 times as long as the exopod, appendix interna 0.49–0.59 times as long as the appendix masculina vs. appendix masculina 0.50 times as long as the exopod, appendix interna 0.25 times as long as the appendix masculina in *C. breviata*); the shorter stylocerite (not reaching the basal antennular segment vs. beyond the basal antennular segment in *C. breviata*); the more slender scaphocerite (about 2.7–3.2 times as long as wide vs. 2.7 times as long as wide in *C. breviata*); more spinules on the uropodal diaeresis (22–26 spinules vs. 16–20 spinules in *C. breviata*); and the larger egg size (0.60–0.66 mm × 1.00–1.10 mm vs. 0.53–0.56 mm × 0.80–0.95 mm in *C. breviata*).

*C. tonggulinensis* sp. nov. also resembles *C. serrata* Stimpson, 1860, in the short rostrum and the male sexual appendages (cf. Liang 2004). However, it can be separated from *C. serrata* by the fewer rostral teeth (unarmed, rarely with one or two dorsal teeth vs. 7–14 dorsal teeth and 1–3 ventral teeth in *C. serrata*); the shorter stylocerite (reaching 0.74–0.80 times the length of the first antennular segment vs. reaching the middle of the second segment in *C. serrata*); more spinules on the flexor margin of the dactylus of the fifth pereiopod (33–42 spines vs. 25–31 spines in *C. serrata*); more spinules on the uropodal diaeresis (22–26 vs. 18–21 in *C. serrata*); and the outermost spicule being longer than the lateral angle (vs. the outermost spicule as long as the lateral angle in *C. serrata*).

*C. tonggulinensis* sp. nov. somewhat resembles *C. baoting* Cai, 2014, which also occurs in Hainan, in the short rostrum and its armature (cf. Cai 2014). However, *C. tonggulinensis* sp. nov. differs from *C. baoting* by the shape of the endopod of the male first pleopod (sub-oval in shape vs. sub-rectangular in shape in *C. baoting*); the longer appendix masculina and appendix interna of the male second pleopod (appendix interna 0.49–0.59 times as long as the appendix masculina, appendix masculina 0.57–0.68 times as long as the exopod vs. appendix interna 0.40 times as long as the appendix masculina, appendix masculina 0.50 times as long as the exopod in *C. baoting*); the more slender chela of the second pereiopod (2.62–2.88 times as long as wide vs. 2.40 times as long as wide in *C. baoting*); more spinules on the uropodal diaeresis (22–26 vs. 20–23 in *C. baoting*), with the outermost spicule longer than the lateral angle (vs. the outermost spicule shorter than the lateral angle in *C. baoting*); and the smaller egg size (0.60–0.66 mm × 1.00–1.10 mm vs. 0.80 mm × 1.40 mm in *C. baoting*).

**Molecular results.** The intraspecific p-distances of COI for the new species were 0.0–0.6%. The new species is most similar to *C. breviata*, with a genetic divergence

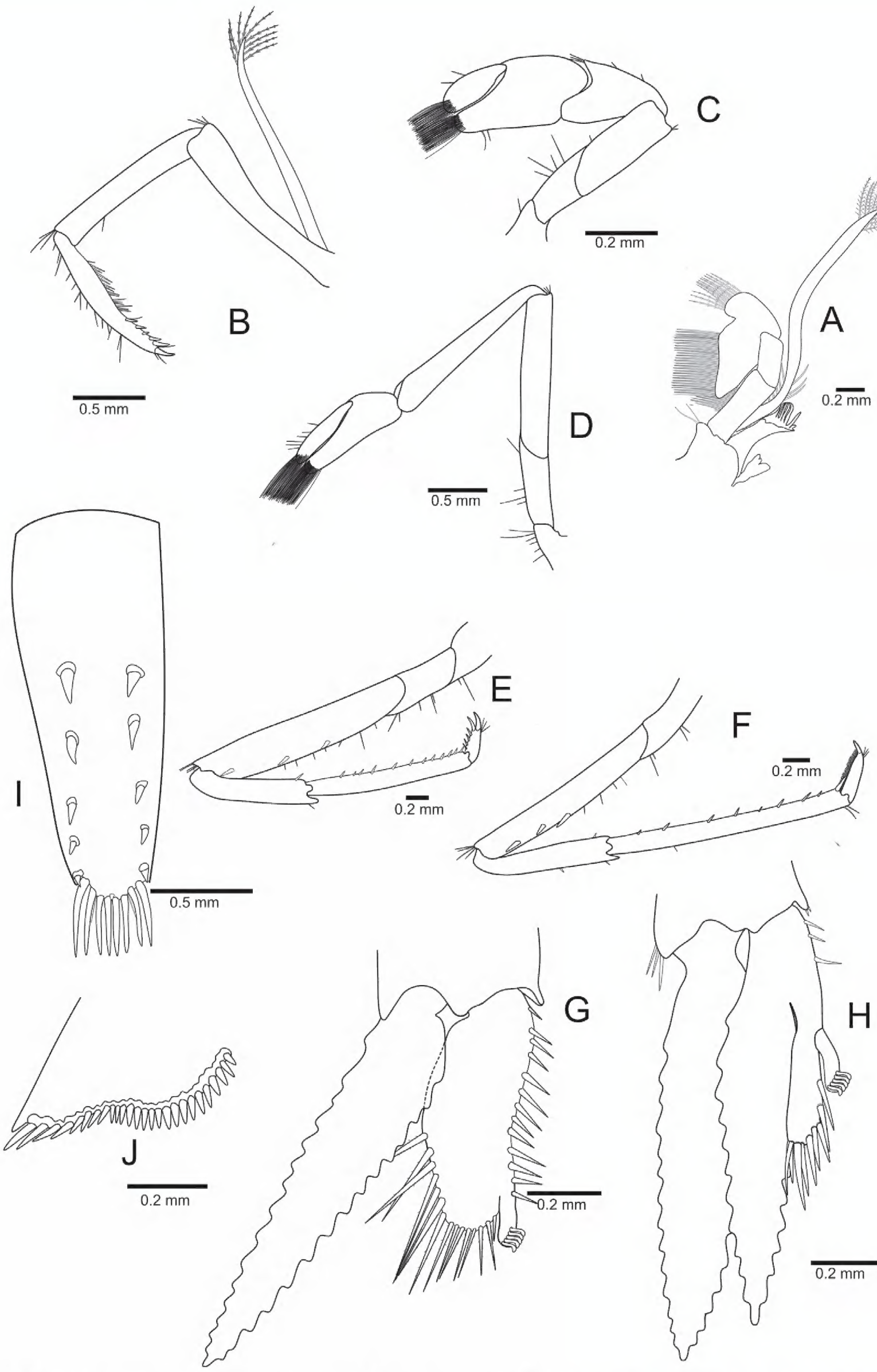


**Figure 3.** *Caridina tonggulinensis* Hou, Zhang & Guo, sp. nov.: **A–J.** Paratype male (CAS5713009). **A.** Second maxilliped; **B.** Third maxilliped; **C.** First pereiopod; **D.** Second pereiopod; **E.** Third pereiopod; **F.** Fifth pereiopod; **G.** First pleopod of the male; **H.** Second pleopod of the male; **I.** Telson; **J.** Uropodal diaeresis.

(p-distance) of 9.6–9.8%, and to *C. baoting* (13.6–13.8%). The intraspecific p-distances of 16S rRNA for the new species were 0.0–0.2%. The new species is most similar to *C. breviata*, with a genetic divergence (p-distance) of 2.3–2.5%, followed by *C. tricincta* (6.5–6.8%), *C. lineatus* (6.5–6.7%), *C. tetrazona* (7.0–7.3%), and *C. serrata* (7.3–7.5%) (Fig. 4, Suppl. material 1, 2).

**Coloration.** Body is translucent reddish-brown; some individuals exhibit blue. The plastron occasionally bears scattered small black spots (Fig. 1C).

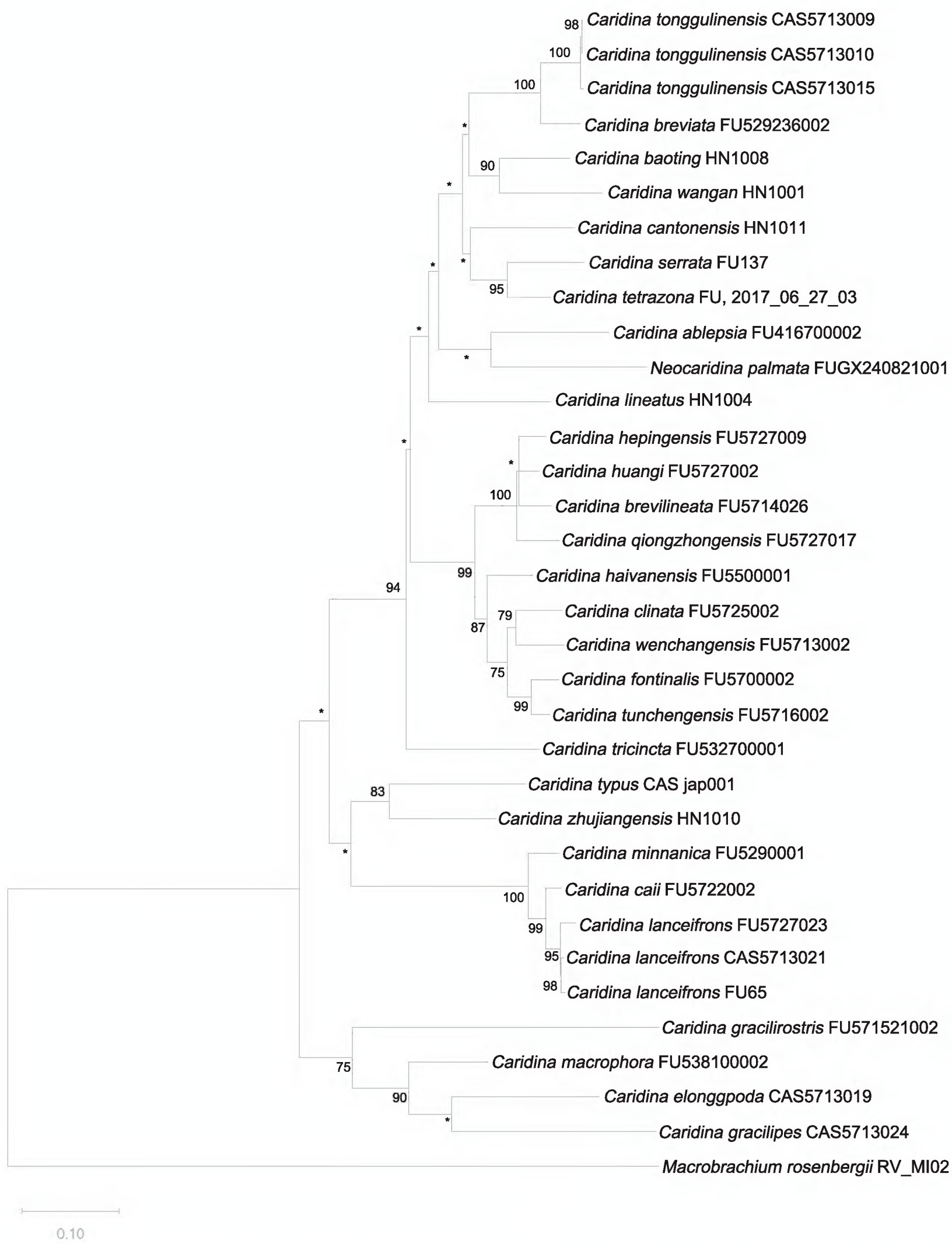


**Figure 4.** Maximum likelihood (ML) phylogenetic tree of the new species of *Caridina* and other atyids, and one *Macrobrachium* species, based on analyses of two mitochondrial gene fragments. The scale bar indicates the substitution rate. The code following each species name represents the specimen code (replaced with * when node support is < 70).

**Ecology notes.** Comprehensive field surveys within and surrounding TNNR indicate that *C. tonggulinensis* sp. nov. is restricted to only five streams in the reserve (Fig. 1, Table 1). These are typical mountain streams, 600–1000 m in length, 0.3–1.0 m in width, and 0.3–0.8 m in depth. Flowing down steep slopes, some exhibit substantial drops of up to 170 m. Flow velocity, governed by the elevation gradient, creates a mosaic of rapid-, moderate-flow, and slow-flow sections along the channel. The substrate consists of large rocks mixed with sand, pebbles, and silt, and the streambed is covered with leaf litter. The riparian zones are formed mostly by shrubs, with dense aquatic grasses along both stream banks. A distinct seasonal hydrological cycle is observed. Water levels are low (~0.3 m) and stable from January to March, reach their peak

(~0.8 m) during the April–June rainy period, and then decline steadily. Due to reduced rainfall and increased evaporation from July onward, some downstream segments can dry up completely.

A 2-year field study revealed a distinct intra-annual abundance pattern in the population dynamics of *C. tonggulinensis* sp. nov., with clear seasonal drivers. The population peaks between January and April, a period driven by the emergence and recruitment of juveniles from the previous year. These juveniles thrive under stable, low-flow conditions—conditions that also promote the accumulation of abundant vegetation debris on the stream bottom, a crucial food source for growth. A significant decline in abundance follows in May and June, primarily driven by the flushing of organic detritus due to increased rainy-season flow, combined with natural post-reproductive mortality. The population decreases sharply throughout the July–December dry season, as stream fragmentation confines it to a few remnant pools that serve as refuges. However, this species exhibits a remarkable capacity for population recovery, enabling it to regenerate and flourish annually, such that interannual differences in abundance are very minor. At multiple collection sites (Table 1), this species co-occurs with the crabs *Apotamonautes hainanensis* Parisi, 1916, and *Neotiwaripotamon whiteheadi* Parisi, 1916.

In addition to population dynamics, *C. tonggulinensis* sp. nov. exhibits distinct reproductive features. It reproduces continuously throughout the year, with two reproductive peaks. The primary peak occurs from April to May, with about 80% of females being ovigerous, whereas the secondary peak occurs from October to December, with approximately 60%. Juveniles first appear in May. By late June, the population becomes dominated by juveniles, as post-spawning adults gradually die off. After growing for 5–6 months, juveniles attain maturity by October and begin to mate and spawn, marking the onset of their first reproductive peak. In late November, juveniles and adults coexist, with adults constituting the majority. This broodstock is capable of reproducing again by the following April, initiating a second breeding peak. A size difference was observed between the two breeding peaks: individuals from the October peak are smaller than those from the subsequent April peak. This observation supports the inference that juveniles require 5–6 months of growth to attain maturity, corresponding to a total lifespan of approximately 1–1.2 years.

**Etymology.** The new species is named after its type locality: Tongguling National Nature Reserve.

**Distribution.** Tongguling National Nature Reserve, Hainan.

## Discussion

Within Tongguling National Nature Reserve, three *Caridina* species were identified: *C. tonggulinensis* sp. nov., *C. lanceifrons*, and *C. elongapoda*. Among these, *C. tonggulinensis* sp. nov. is recognized as a new species, a conclusion supported by both morphological and molecular evidence.

Both *C. elongapoda* and *C. lanceifrons* are distributed along the southern coast of China. *C. elongapoda* also occurs in Malaysia, Borneo, and the Philippines, primarily in estuarine habitats, whereas *C. lanceifrons* ranges from central China to Vietnam and Thailand and inhabits brackish to freshwater environments.

*C. tonggulinensis* sp. nov. is a landlocked species endemic to Tongguling National Nature Reserve, characterized by low fecundity and large egg size despite its proximity to the coast. Reproduction in this species is continuous throughout the year, following a bimodal pattern with peaks in April–May and October–December. Over a lifespan of 1–1.2 years, a single female can produce three to five broods.

*C. lanceifrons* and *C. elongapoda* are commercially important. *C. lanceifrons* is used locally for both poultry feed and human consumption, whereas *C. elongapoda* is often captured by enthusiast breeders in coastal China and sold on the market as a "Native Red Nose Shrimp."

*C. tonggulinensis* sp. nov. faces significant threats even within protected areas, primarily from hydrological alteration and habitat change. Due to its extremely restricted distribution and low abundance, compounded by multiple threats, this species should be assigned a high conservation priority. Concurrently, population monitoring and comprehensive ecological, biological, and genetic investigations should be initiated.

Under the IUCN Red List Categories and Criteria (https://www.iucnredlist.org/resources/categories-and-criteria), *C. tonggulinensis* sp. nov. has been found only in the type localities. With no current information on its potential broader distribution, it is therefore assessed as Data Deficient (DD). *C. elongapoda* and *C. lanceifrons* have been assessed as Least Concern on the IUCN Red List (De Grave 2013a, 2013b) due to their large distributional ranges.

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# Supplementary material 1

## *p*-distance for *COI* for all relevant species

Authors: Jiping Zhang, Junjie Hou, Jinjin Fan, Yixinran Xu, Qinghua Chen, Zhaoliang Guo

Data type: xlsx

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Link: https://doi.org/10.3897/zse.102.179487.suppl1

# Supplementary material 2

## *p*-distance for 16S for all relevant species

Authors: Jiping Zhang, Junjie Hou, Jinjin Fan, Yixinran Xu, Qinghua Chen, Zhaoliang Guo

Data type: xlsx

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